CRYPTOCORYNE BECKETTII COMPLEX (ARACEAE) INTRODUCED AT A FLORIDA SPRING

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ABSTRACT

A vegetative population of *Cryptocoryne* (Araceae), introduced at a Florida spring, appeared to represent three closely related species in the *C. beckettii* complex: *C. beckettii Thw.* ex Trimen, *C. wendtii* de Wit and *C. undulata* Wendt. Individuals of *C. undulata* were true to type and could be delineated at the site. Intergradation of diagnostic features was common in others, upon transplanting and flowering. While some transplants produced spathes characteristic of either *C. wendtii* or *C. beckettii*, intermediates between the two species were common. Neither *C. beckettii* nor *C. wendtii* could be delineated at the site. The seclusion of the stream and the integrity of native plant communities have likely prevented dispersal downstream.

RESUMEN

Una población vegetativa de *Cryptocoryne* (Araceae), introducida en un manantial de Florida, al parecer representa tres especies estrechamente relacionadas del complejo *C. beckettii*: *C. beckettii* Thw. *ex* Trimen, *C. wendtii* de Wit y *C. undulata* Wendt. En el lugar de estudio, fueron clasificados como verdaderos tipos ejemplares de *C. undulata*. En otros ejemplares, después del transplante y floración, fue común observar intergradación de caracteres diagnósticos. Aún cuando algunos transplantes produjeron espatas, características de *C. wendtii* o de *C. beckettii*, fue común observar ejemplares con características intermedias de ambas especies. Las especies *C. beckettii* y *C. wendtii* no fueron delineadas en el sitio de estudio. La condición de aislamiento del manantial y la condición íntegra de las comunidades de plantas nativas han impedido probablemente la dispersión corriente abajo.

INTRODUCTION

Cryptocoryne Fisher ex Wydler are highly sought-after and commercially marketed as decorative plants for tropical aquariums. The most commonly cultivated species belong to the *C. beckettii* complex, a uniform and specialized group endemic to Sri Lanka (Jacobsen 1977; Jacobsen 1987; de Graaf & Arends 1986).

In their native range, members of the *Cryptocoryne beckettii* complex inhabit pristine rivers and springs. In some areas, they form large submersed or emergent stands (Jacobsen 1987), although some populations have declined from commercial collecting and habitat destruction (de Graaf & Arends 1986). Species in this group commonly root in the sand and silt that overlay rocky, shallow streambeds (de Graaf & Arends 1986; Rataj & Horeman 1977) and occupy shady, sheltered niches rarely inhabited by other plants (Jacobsen 1977; Doyle 2001). They adapt readily to terrestrial conditions and flower with water draw down, when leaves become emersed and the roots well aerated (Jacobsen 1977; Clark 1991). Vegetative reproduction is important in population establishment and expansion (Jacobsen 1977). In cultivation, *C. beckettii* members are hardy and vigorous, propagating abundantly by rhizomes and stolons, and enduring hard, calcium rich water (Miller 1998; Rataj & Horeman 1977).

In treating *Cryptocoryne* for the Flora of Ceylon, Jacobsen (1987) portrayed four species as closely related within the *Cryptocoryne beckettii* complex: *Cryptocoryne walkeri* Schott, *C. beckettii* Thw. ex Trimen, *C. wendtii* de Wit, and *C. undulata* Wendt. Although mainly diploids, all four have been found as triploid species and several combinations within the complex have resulted in the formation of hybrids (Jacobsen 1977; Arends et al. 1982; Jacobsen 1987). Because *Cryptocoryne* share many similarities in their vegetative features, an inflorescence is requisite for species identification. Determination of the species in the *C. beckettii* group rests on subtle differences in the morphology of the spathe, which is a fleshy, ornate bract enclosing the inflorescence. Key features of the spathe include the size and color of the collar and the shape and degree of twist of the terminal limb. Since differences in these characters are essentially quantitative, it has been recognized that the four taxa could prove to constitute a single species (Jacobsen 1987).

Wunderlin's (1998) inclusion of *Cryptocoryne wendtii* de Wit as an introduced component of the Florida flora was the first recording of this Southeast Asian genus for North America. Soon after, Rosen (2000) reported *C. beckettii* Thw. ex Trimen as introduced to Texas, followed by Doyle (2001) who detailed its expansion and spread in the upper spring-fed regions of the San Marcos River.

Rosen's description of *C. beckettii* from the San Marcos River, Texas, was based on vegetative material (Rosen 2000). Doyle (2001) reported that *C. beckettii* had been adequately confirmed in Texas after K. Sanders and D. Lemke identified flowering transplants. Wunderlin's report of *C. wendtii* in Florida was similarly based on a sterile specimen collected at Rainbow Springs Aquatic Preserve, Florida, in 1989. The objective of this inquiry was to confirm the persistence of *Cryptocoryne* at Rainbow Springs Aquatic Preserve and to collect material for cultivation and subsequent species determination from flowering plants.

The Rainbow River is a karstic, spring-fed stream receiving artesian groundwater that is high in clarity, rich in soluble carbonates and moderate in temperature (USGS 1999). The run traverses 8 km before joining the Withlacoochee River near the town of Dunnellon. A site of exceptional scenic beauty and a popular destination for recreation, it was designated the Rainbow Springs Aquatic Preserve in 1986 (Florida Statute 258.39 [32]).

METHODS

In May 2000 and in June 2001, approximately 50 individuals were uprooted from the *Cryptocoryne* colony found at Rainbow Springs Aquatic Preserve. Four sided, open-ended aluminum units (0.25 m^2) enclosed in double netting were placed over each area during sampling to delineate the sampling area and to trap stray plant fragments. Sampling attempted to localize variation observed in leaf color and in total represented seven areas within the colony. Samples were transplanted to 10 cm pots in a bark and peat-based potting medium and cultivated out of water, outdoors, with shade and screening, during the warmer months. Transplants established readily, losing submersed leaves and producing new terrestrial foliage. Pots were moved to a heated greenhouse when nighttime temperatures dropped below 10°C. Flowering began in December and continued through July. The inflorescences survived for several days and were documented with photographs and voucher specimens before decline. On pressing and drying, the inflorescences lost color and the angle of terminal limbs appeared more upright. Photography provided for better study than did prepared specimens. Species identification was based on Jacobsen (1987).

To assess plant density, the extent of subsurface rhizomes, and the potential of hand removal as a control method, total vegetation was harvested from two 0.25 m^2 areas within the colony. Limestone gravel was removed with fingers as necessary to extract plants in whole (i.e. with basal parts and some extent of rhizomes intact). Roots were harvested to approximately 10 cm deep. Top portions of plants were separated from subsurface material (roots). Weight was taken before and after material was oven dried at 60°C.

Adjacent, sterile colonies of *Myriophyllum* and Cyperaceae were sampled for subsequent transplanting, flowering and identification. *Myriophyllum* was tank cultivated in 50 cm of water, the sedge was grown under terrestrial conditions.

RESULTS AND DISCUSSION

Cryptocoryne was found persisting and well established at Rainbow Springs Aquatic Preserve, in a shaded cove of a spring fed stream. The plants grew submersed in an area of approximately 130 m^2. Water depth ranged from 28 to 75 cm, although outlying runners extended to crevices as deep as 150 cm. The low growing plants reached an average height of 7 cm. The vegetation consisted of dense mats that grew to the exclusion of other macrophytes.

Transplants from the *Cryptocoryne* colony produced approximately 100 inflorescences. Voucher specimens and photographs documented 49 representative inflorescences. Twenty-five appeared characteristic of three species in the *C. beckettii* complex: *C. undulata*, *C. beckettii*, and *C. wendtii* (Fig. 1–3). However, 20 were intermediate between *C. beckettii* and *C. wendtii*. *Cryptocoryne*

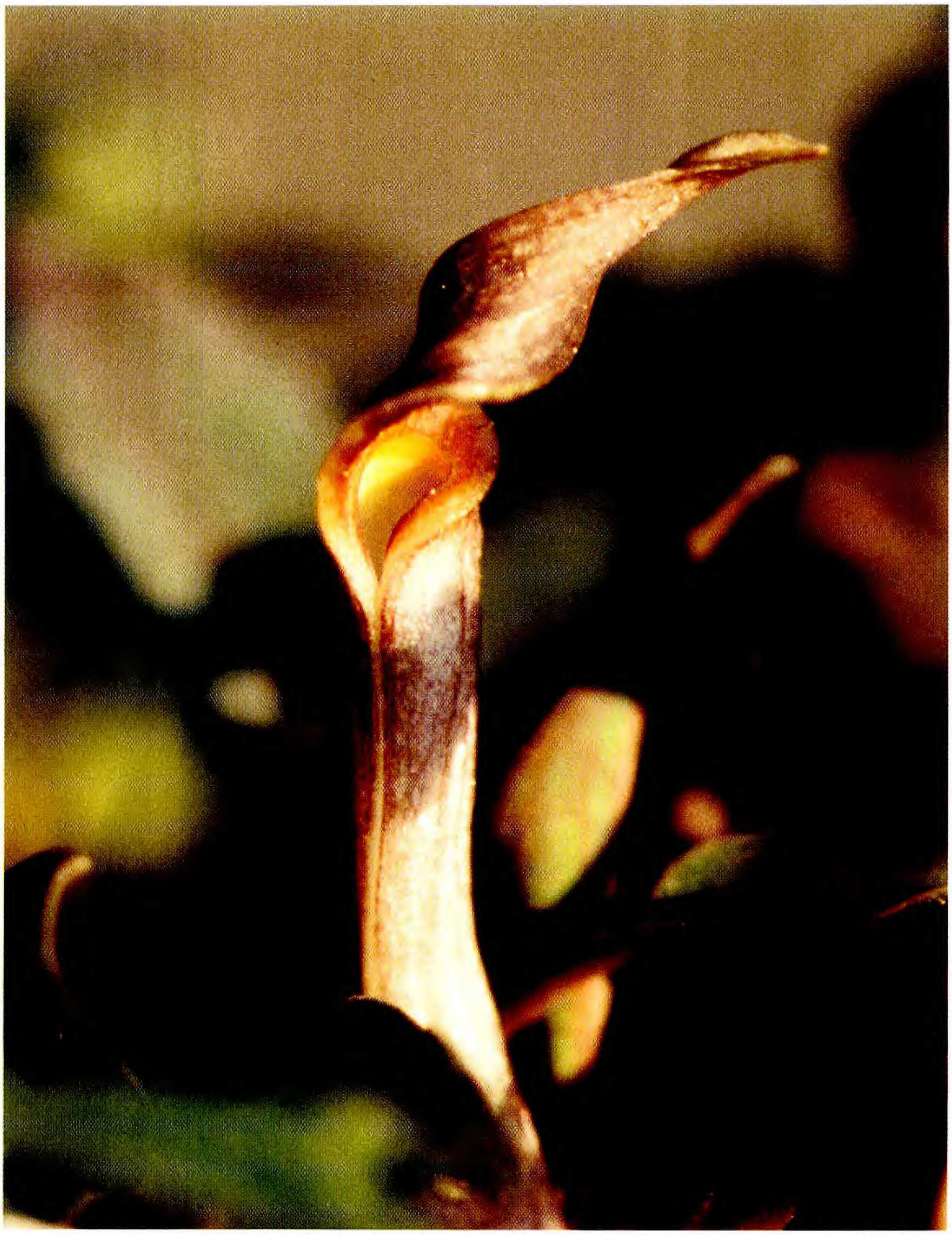


Fig. 1. ***Cryptocoryne undulata*** **Wendt.**

undulata was the only species that could be delineated at the Preserve. The remaining, and predominant, vegetation at the site could not be delineated as either *C. beckettii* or *C. wendtii*.

FIG. 2. *Cryptocoryne wendtii* de Wit.

Spathes of *C. undulata* were uniform in color and morphology. The collar zone graded from yellow to cream and the terminal limb darkened from yellow to golden brown upon maturing. The terminal limb was always nearly doubly twisted and positioned diagonally to the axis of the spathe tube. *Cryptocoryne undulata* was delineated within a small (approx. $4m^2$), distinct region of the colony. Submersed, unopened inflorescences found within this region were similarly yellow at the collar zone and on the inside of the unfurled limb.

Submersed leaf blades of *C. undulata* were narrowly lanceolate. They ranged in length from 4.0 to 9.0 cm (mean 6.1, SD 1.5) and in width from 0.7 to 1.8 cm (mean 1.3, SD 0.4). Bases were cordate to cuneate and the entire leaf margin was crisped. Submersed leaf color was dark brownish green on the adaxial surface; abaxial sides and petioles were maroon. Terrestrial plants of *C. undulata* produced smaller lanceolate leaves with acuminate bases and margins that were crisped only along the leaf base. Terrestrial leaf color was deep green with veins and petioles red.

While four transplants produced spathes characteristic of *C. wendtii*, and 17 characteristic of *C. beckettii*, more than 20 individuals appeared intermediate and could not be determined to the species level. Jacobsen (1987) separated *C. beckettii* from *C. wendtii* by the angle on the terminal limb of the spathe. The limb of *C. beckettii* is more upright or sub-erect, and twisted to recurved while that of *C. wendtii* is obliquely twisted, often extending into a tail (Jacobsen 1987). Jacobsen (1976) noted these characters as difficult to describe and variable, partly in response to environmental conditions. In the present study, the key characters were found to intergrade across a population grown under greenhouse conditions. The angle of the terminal limb (as measured from the spathe tube) ranged widely from 93°to 175°(Table 1). Limbs assumed different shapes, as well as angles, and spathes frequently shared diagnostic features. For example, spathes with sub-erect limbs (limbs not obliquely twisted) were found extending into well-defined tails (Fig. 4b).

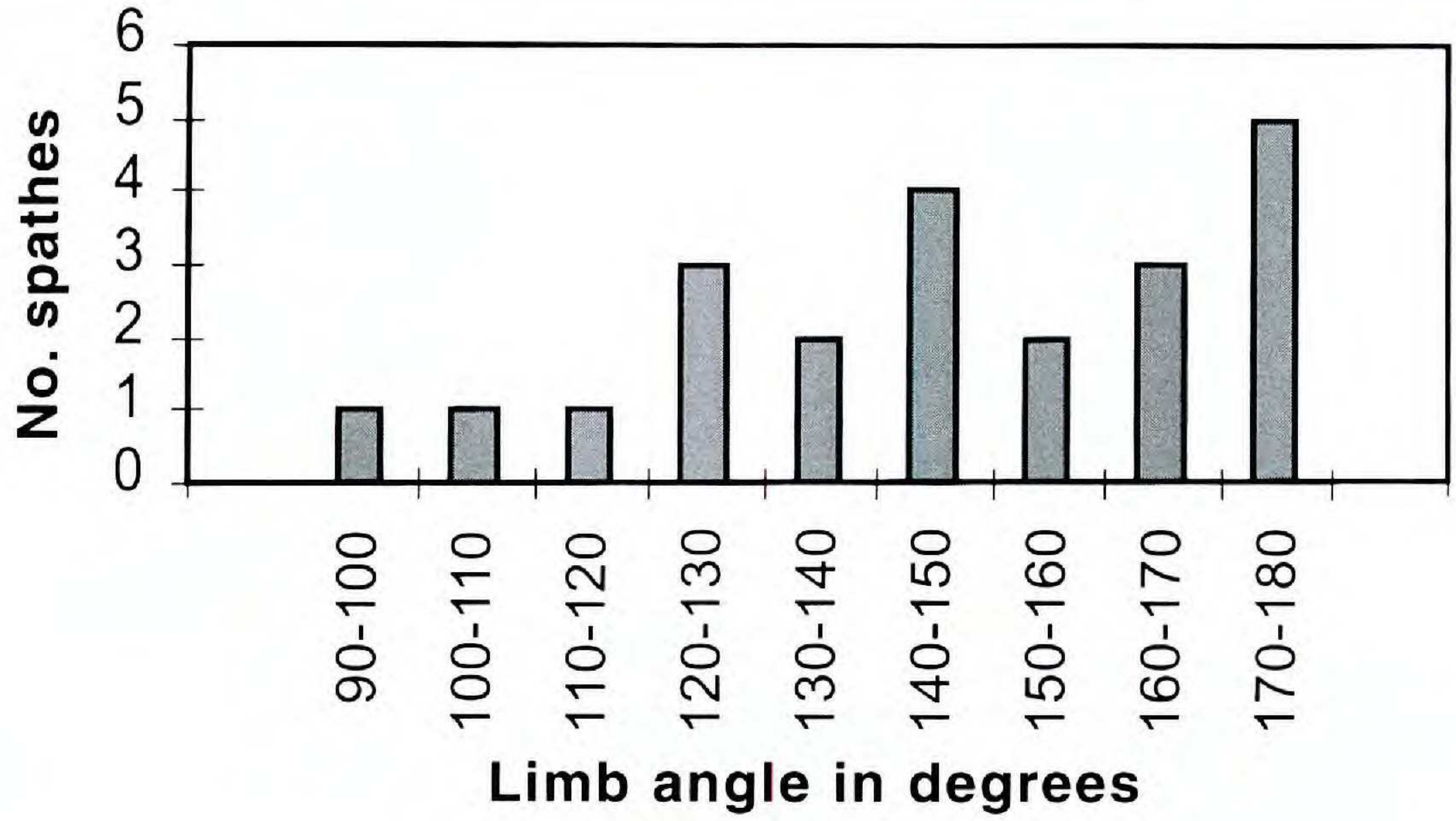
Jacobson (1976; 1987) further depicted the terminal limbs of *C. beckettii* as yellowish to brownish and those of *C. wendtii* as yellowish to purplish brown. In this study limbs varied in color from golden to green to greenish or purplish brown. On occasion they darkened with maturity. Limb color did not always correlate with limb position, for example, greenish brown limbs ranged from more erect to nearly perpendicular (Fig. 4d) and true green limbs were found twisted at an angle (Fig. 4a). Thus, in form and color many individuals in this study appeared intermediate between *C. beckettii* and *C. wendtii*.

The identity of those individuals that could be determined according to floral characteristics was often in question when apparently distinct individuals (*C. beckettii* and *C. wendtii*) were traced back to the same sampling block at the Preserve (Fig. 5 and representative specimens *Jacono 373* vs. *Jacono 368*). As a result, clear clonal populations, although expected for long established, vegetatively reproducing plants, could not be delineated for either *C. beckettii* or *C. wendtii*.

Submersed inflorescences found in sunny shallow areas had purple collar zones and green inner limbs. However, with spathes tightly furled, they contributed little in separating *C. beckettii* from *C. wendtii*, and merely confirmed the ability of this type to flower *in situ*.

Plants of this type (*C. beckettii*, *C. wendtii*, and the intermediates) demonstrated differences in leaf color while growing at the Preserve. Submersed leaf color of the adaxial surfaces varied from green marbled with brown to pink infused with green venation. Abaxial sides were violet to pink. This color variation was apparent in zones and may be attributed to factors of substrate and sunlight at the site. Green-brown plants grew in organic sediment under continuous shade of the tree canopy; pink plants grew on limestone substrate in zones of higher sunlight. After transplanting, the terrestrial leaves that replaced the submersed vegetation were without variation and uniform in color. The submersed leaves were lanceolate to ovate with cordate bases and sinuous margins. The length of their leaf blades ranged from 3.8 to 9.6 cm (mean 6.2, SD 1.5)

Table 1. Distribution of limb angles (measured from the spathe tube) of 22 inflorescences photographed.



and their width measured 1.1 to 3.3 cm (mean 2.2, SD 0.6). Terrestrial leaves were smaller and narrowly ovate with cordate bases, olive-green adaxial surfaces and violet on the abaxial side.

Variability and intergradation of the features upon which these species are based prevented delineation of *C. beckettii* from *C. wendtii*. While certain individuals seemed easy to place to the species level, they could not be traced back to distinct areas at the site. Other individuals were intermediate and could not be determined to species. Regardless of spathe morphology, terrestrially grown transplants within this type were consistently uniform in vegetative features. The predominating *Cryptocoryne* material at the Preserve can only be described as *C. beckettii* sensu lato.

The *Cryptocoryne* subsurface biomass consisted of large amounts of roots, rhizomes and stolons that were difficult to uproot by hand. Roots were well entrenched in contrasting substrates: silty, organic sediment near the shoreline and pebbled to rocky limestone extending into the stream.

Plant density values were 1480 plants / m^2 for *Cryptocoryne beckettii* s.l. and 1880 plants / m^2 for *C. undulata*. Dry roots of *C. beckettii* s.l. weighed nearly four times more than dry top growth: dry roots of *C. undulata* weighed eight times that of corresponding top growth (Table 2).

Like many aroids, *Cryptocoryne* employ contractile roots to adjust plant level after heaving or flooding (Bown 1988). Tiny rootlets sent deep into the rock use root pressure to contract in length and pull the roots farther into the

Fig. 3. *Cryptocoryne beckettii* Thw. ex Trimen.

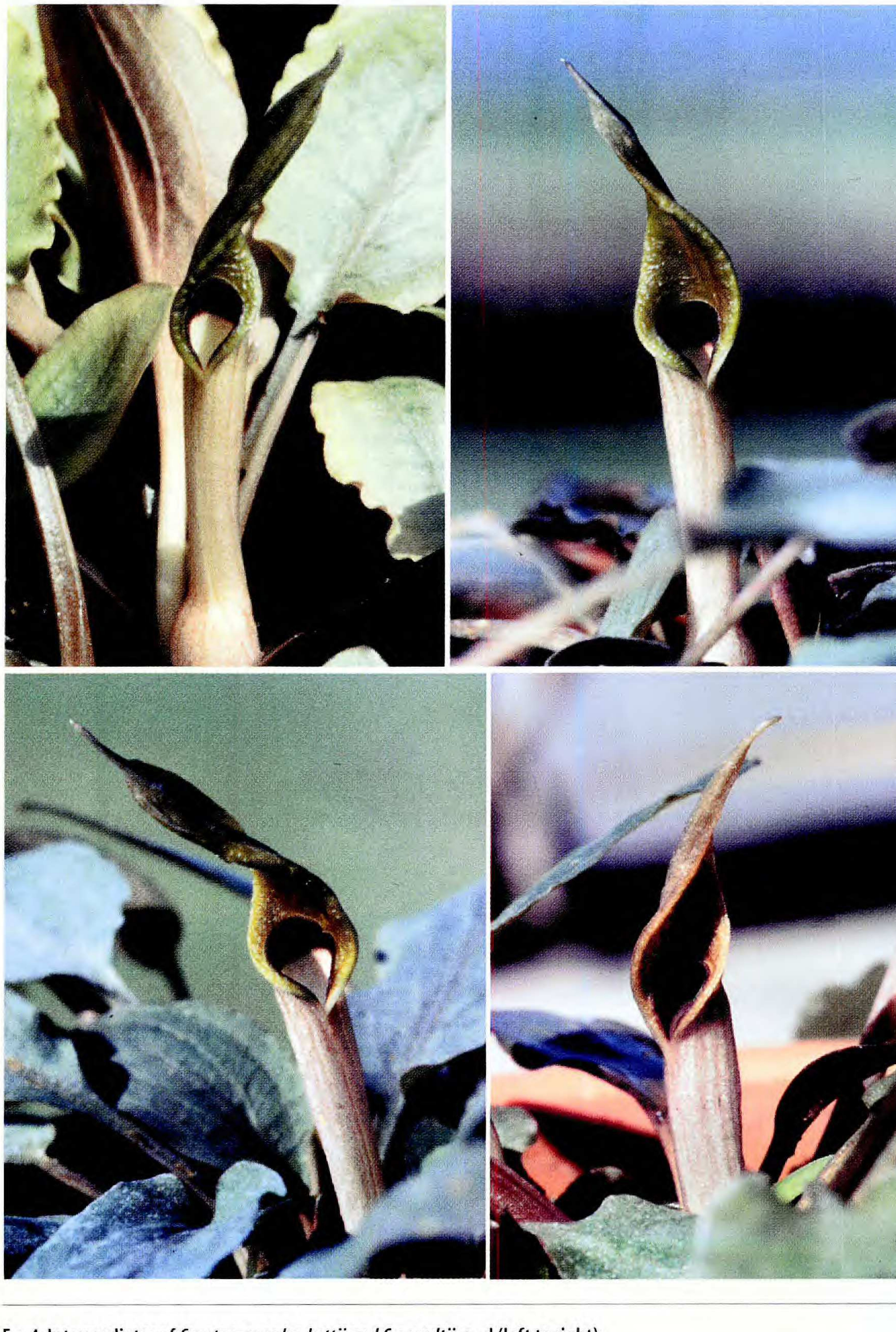


Fig. 4. Intermediates of *Cryptocoryne beckettii and C. wendtii*, a–d (left to right).

TABLE 2. Plant density and top to root growth, per m^2 of submersed plants.

	No. of plants	Top fresh wt. in g	Top dry wt. in g	Roots fresh wt. in g	Roots dry wt. in g	Roots/ Top
Cryptocoryne undulata	1880	349g	23.2 g	1007g	183.8g	7.9
Cryptocoryne beckettii s.l.	1480	251g	20 g	426g	74g	3.7

substrate. This adaptation firmly anchors plants in swift currents and likely accounts for the deep rooting in limestone substrate at the Preserve, complicating mechanical removal without destructive draglines or dredging.

Shortened runners, basal shoots, were formed at the base of both submersed and transplanted material of all three species. Jacobsen (1987) described these "bulbil-like runners" on forms of *C. wendtii* and *C. undulata*, but did not report them for *C. beckettii*. Small (< 5mm), abundant (up to 8–20 per individual), and fragile, the shoots are loosely associated with the mother plant and readily break off. They quickly develop an initial root and primary leaf to establish as new plants. Kane et al. (1999) successfully employed basal shoots for the *in vitro* propagation of *C. wendtii*. At the Preserve, basal shoots were abundant in springtime. In transplants, they provided the flush of new season growth after spring flowering. Walking on submersed plants can dislodge basal shoots, which immediately sink to the bottom. Conversely, dislodged rhizomes float on the water surface. Because of their abundance and small size, the shoots are difficult to contain and may be carried downstream with bottom currents; they may be more effective than rhizome fragments as propagules for downstream spread.

Reproduction in *Cryptocoryne*, like other submersed macrophytes, is primarily accomplished through vegetative structures. Rhizomes, runners (stolons) and basal shoots provide multiple means for expansion of an apparently well-suited population at Rainbow Springs Aquatic Preserve.

Submersed inflorescences were observed in April and June on both types of *Cryptocoryne* at the Preserve. In their native range, *Cryptocoryne* commonly grow submersed during rainy periods and emerge to flower when seasonal water levels drop (Jacobsen 1977). Submersed inflorescences, while not uncommon in nature, must emerge to be insect pollinated before forming seeds. Typically short-lived, the seeds may be dispersed in water but are not vectored long distances over land (Bown 1988; Jacobsen 1976; Bogner 1987). Constant water level ensured by the spring flow should keep the inflorescences of submersed plants underwater. However, species in the *C. beckettii* complex are well adapted to terrestrial life (Jacobsen 1977) and runners could establish amphibious plants that might flower along the damp, shady shoreline at the Preserve.

Cryptocoryne was found encroaching on adjacent *Sagittaria kurziana* Glück, *Myriophyllum heterophyllum* Michx. and a continually inundated population of *Rhynchospora colorata* (L.) H. Pfeiff. Several meters downstream, *Zizania aquatica* L., *Rorippa floridana* Al-Shehbaz & Rollins, *Ludwigia repens* J.R. Forst., *Sagittaria lancifolia* L., *Hydrocotyle umbellata* L., *Chara, Fontinalis, Utricularia, and Leersia* spp. contributed to one of the few intact aquatic communities remaining at the Preserve. The natural vegetation may curtail the downstream spread of *Cryptocoryne* by trapping dislodged rhizomes and shoots. Extensive underwater monitoring conducted in 1996 and 2000 detected no additional sites with *Cryptocoryne* at Rainbow Springs Aquatic Preserve (P. Sleszynski, pers. comm.).

Assessing Risks

In North America, weedy infestations of *Cryptocoryne beckettii* sensu lato may be limited to karstic spring environments of the southern states. Laboratory experiments demonstrated that four *Cryptocoryne* species, *C. affinis* Hook.f., *C. cordata* Griffith, *C. elliptica* Hook.f. and *C. minima* Ridley, effectively used bicarbonate as the main carbon source when pH ranged between 7.5 and 9.1 (Cheng and Mansor 2000). In high pH (>7.0), hard water systems, relatively large amounts of dissolved inorganic carbon exist as bicarbonate (Spencer and Bowes 1990). At Rainbow Springs Aquatic Preserve the spring water is consistently alkaline and carbonate-rich. Within the last decade pH ranged from 7.87 to 8.27 (USGS 1999). Total hardness value, last determined in 1980, was 58 mg/L, measured as calcium carbonate, and noncarbonate hardness was 3 mg/L, expressed as equivalents of calcium carbonate, indicating a high level of carbonate in the water (USGS 1999). Similar pH values (7.6 to 8.0) were recorded near the headspring of the San Marcos River, although hardness values were not determined (USGS 2000). The ability of *Cryptocoryne* to selectively use bicarbonate under alkaline conditions may contribute to its successful colonization at karstic spring-fed streams in Florida and Texas.

The original *Cryptocoryne* "mother plants" were probably planted at Rainbow Springs Aquatic Preserve before 1986 when the system came under state ownership. Now well established, its potential for dispersal there is considerable. In the San Marcos River, disturbance caused by wading and sporting activities are suspected to contribute to the proliferation of *Cryptocoryne beckettii* downstream (P. Power, U.S. Fish and Wildlife Service, San Marcos, Texas, pers. comm.). Owens et al. (2001) reported a significant increase in dislodged plant fragments below high recreation use areas on the San Marcos River. Likewise, recreational activities were reported as significant in the uprooting of large masses of vegetation in Rainbow River (Mumma et al. 1996). The secluded stream harboring *Cryptocoryne* at Rainbow Springs Aquatic Preserve is currently restricted, but under consideration for public use.

Original voucher specimen. ***Cryptocoryne wendtii*** de Wit, **U.S.A. FLORIDA, Marion Co.:** Dunnellon, Rainbow Springs Aquatic Preserve, quiet spring runs along the Rainbow River, lvs pink/green, frequent, 24 Apr 1989, *Joe Hinkle s.n.* (FLAS), Det: Walter Driggers.

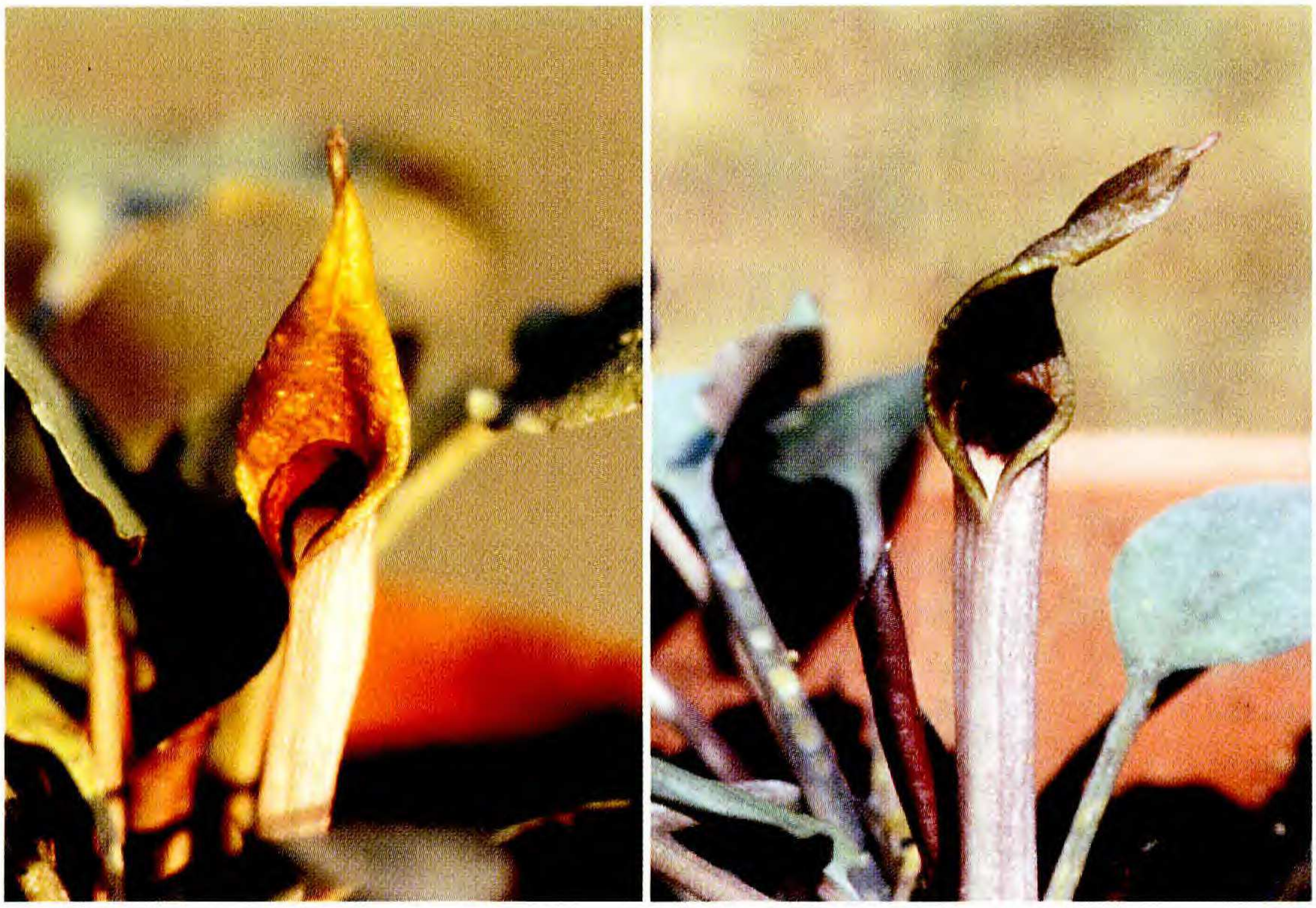


FIG. 5. Apparently distinct individuals transplanted from the same sampling area at the Preserve.

Representative specimens from this study: **U.S.A. Florida. Marion Co.**, Dunnellon, Rainbow Springs Aquatic Preserve, spring run along the Rainbow River.

Cryptocoryne undulata Wendt—Submersed to 75cm at site, sterile: 11 Apr 2001, *Jacono 253* (FLAS, MO); 12 Jun 2001, *Jacono 280* (FLAS). Submersed to 75cm at site, fertile with spathes closed: 11 Apr 2001, *Jacono 254* (FLAS). Flowering in cultivation: 10 Apr 2001, *Jacono 282* (MO); 31 July 2001, *Jacono 296* (FLAS); Apr 2002, *Jacono s.n.* (FLAS); 7 Apr 2002, *Jacono 408* (FLAS).

Cryptocoryne beckettii Thw. ex Trimen—Flowering in cultivation: 17 Dec 2001, *Jacono 368* (MO); 18 Feb 2001, *Jacono 211* (FLAS); 7 Apr 2001, *Jacono 231* (FLAS); 7 Apr 2001, *Jacono 233* (MO); 16 Apr 2001, *Jacono 245* (FLAS).

Cryptocoryne wendtii de Wit—Flowering in cultivation: 14 Feb 2001, *Jacono 210* (FLAS); 29 Feb 2001, *Jacono 216* (FLAS); 27 Jan 2002, *Jacono 373* (MO).

Cryptocoryne beckettii sensu lato—Submersed to 28 cm at site, sterile: 11 Apr 2001, *Jacono 249*, (FLAS); 12 Jun 2001, *Jacono 275* (MO). Submersed to 28 cm at site, fertile with spathe closed, 11 Apr 2001, *Jacono 250* (MO); 12 June 2001, *Jacono 276* (FLAS). Flowering in cultivation with spathes apparently intermediate between *C. beckettii* and *C. wendtii*: 16 Apr 2001, *Jacono 243* (MO); 16 Apr 2001, *Jacono 244* (FLAS); 21 Feb 2001, *Jacono 247* (FLAS); 21 Feb 2001, *Jacono 271* (FLAS); 20 Feb 2002, *Jacono 379* (FLAS); 26 Mar 2002, *Jacono 402* (FLAS).

Myriophyllum heterophyllum Michx.—Submersed plants, rooted, sterile, 19 May 2000, *Jacono 140* (FLAS); Cultivated plants from sterile collection (*Jacono 140*) flowering and fruiting, 20 May 2001, *Jacono 270* (FLAS).

Rhynchospora colorata (L.) H. Pfeiff.—Sterile plants submersed in ca. 70 cm of clear, flowing spring water, 12 Jun 2001, *Jacono 281* (FLAS); Cultivated plants from sterile collection (*Jacono 281*) flowering and fruiting, 8 Oct 2001, *Jacono 360* (NY; FLAS)].

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REFERENCES

Arends, J.C., J.D. Bastmeijer and N. Jacobsen. 1982. Chromosome numbers and taxonomy in *Cryptocoryne* (Araceae). II. Nordic J. Bot. 2:453–463.

Bogner, J. 1987. Morphological variation in Aroids. Aroideana 10:4–16.

Bown, D. 1988. Aroids: plants of the arum family. Timber Press, Portland.

Cheng, H.S. and M. Mansor. 2000. A comparative study on the acquisition of inorganic carbon by four native aquatic plants from the genus *Cryptocoryne* and an aquatic weed *Hydrilla verticillata*. Malaysian Appl. Biol. 29:43–53.

Clark, R. 1991. Flower and seed production in *Cryptocoryne*. Aquatic Gardener 4(1):7–14.

de Graff, A. and J.C. Arends. 1986. The occurrence of *Cryptocoryne* and *Lagenandra* (Araceae) on Sri Lanka. Nord. J. Bot. 6:757–764.

Doyle, R.D. 2001. Expansion of the exotic aquatic plant *Cryptocoryne beckettii* (Araceae) in the San Marcos River, Texas. Sida 19: 1027–1038.

Jacobsen, N. 1976. Notes on *Cryptocoryne* of Sri Lanka (Ceylon). Bot. Not. 129:179–190.

Jacobsen, N. 1977. Chromosome numbers and taxonomy in *Cryptocoryne* (Araceae). Bot. Not. 130:71–87.

Jacobsen, N. 1987. *Cryptocoryne*, in M.D. Dassanayake, ed. A revised handbook to the flora of Ceylon. Amerind Publishing Co. Pvt. Ltd., New Delhi.

Kane, M.E, G.L. Davis, D.B. McConnell and J.A. Gargiulo. 1999. *In vitro* propagation of *Cryptocoryne wendtii*. Aquatic Bot. 63:197–202.

Miller, R. 1998. Caring for groups of *Cryptocorynes* or waylaying your wandering *wendtii*. Aquatic Gardener 11:187–189.

Mumma, M.T., C.E. Cichra, and J.T. Sowards. 1996. Effects of recreation on the submersed aquatic plant community of Rainbow River, Florida. J. Aquatic Pl. Mangem. 34:53–56.

Owens, C.S., J.D. Madsen, R.M. Smart, and R.M. Stewart. 2001. Dispersal of native and nonnative aquatic plant species in the San Marcos River, Texas. J. Aquatic Pl. Mangem. 39: 75–79.

Rataj, K. and T.J. Horeman. 1977. Aquarium Plants: their identification, cultivation and ecology. T.F.H. Publications, Inc., Neptune, New Jersey.

Rosen, D.J. 2000. *Cryptocoryne beckettii* (Araceae), a new aquatic plant in Texas. Sida 19: 399–401.

Spencer, W. and G. Bowes. 1990. Ecophysiology of the world's most troublesome aquatic weeds. In A.H. Pieterse and K.J. Murphy (Ed.). Aquatic weeds, the ecology and management of nuisance aquatic vegetation. Oxford University Press, Oxford.

USGS. 1999. United States Geological Survey Water Quality Database (http://water.usgs.gov/nwis/qwdata).

USGS. 2000. United States Geological Survey Water Quality Database (http://waterdata.usgs.gov/tx/nwis).

Wunderlin, R.P. 1998. Guide to the vascular plants of Florida. University Press of Florida, Gainesville.